5

Patterns of Plant Species Richness Within Families and Genera in Lowland Neotropical Forests: Are Similarities Related to Ecological Factors or to Chance?

Pablo R. Stevenson[1], María Clara Castellanos[2] and Juliana Agudelo T.[1]
[1]*Departamento de Ciencias Biológicas, Universidad de los Andes, Bogotá,*
[2]*Consejo Superior de Investigaciones Científicas,*
Centro de Investigaciones sobre Desertificación (CSIC-UV-GV), Valencia,
[1]*Colombia*
[2]*España*

1. Introduction

Present-day communities are the result of speciation, extinction, and migration (Leigh et al., 2004). Hence, the final outcome of these processes, the assemblage of species present at a site, has been sieved by both ecological and stochastic factors through time (Kristiansen et al., 2011; Stropp et al., 2009). Palinological evidence has demonstrated a correlation between Neotropical floral diversity and climatic change throughout the Cenozoic, showing the highest diversity in the Eocene during periods with high temperatures and an extensive area of tropical forests (Jaramillo et al., 2006). These results imply that present day communities are incomplete "museums" of plant diversity, which have suffered extinctions either through deterministic or stochastic effects. Then, findings from paleoecological studies suggest direct or indirect effects of macro-ecological factors, such as temperature and forested area, determining patterns of plant diversity in the tropics (Fine & Ree, 2006), and reveals patterns of species accumulation during hot and humid periods.

We still know little about the ecological and biogeographical factors that promote species diversification in plants. Plant-animal interactions, such as pollination and seed dispersal, have been proposed as mechanisms that promote plant diversification (Gentry, 1988). However, strict specializations are not common in pollination systems and the role of pollinators in generating diversification of plant species has not been supported (Gravendeel et al., 2004; Waser et al., 1996), although preferences may occur (Gong & Huang, 2011). Recent studies have suggested that habitat specialization to contrasting soil types, mediated by tradeoffs in strategies to avoid herbivory, has occurred in lowland Amazonian plants (Fine et al., 2006). Currently, among many theories to explain plant coexistence in diverse tropical forests at local scales, there are four hypotheses well supported which involve niche differentiation, infrequent competition among understory plants, host specific pests, and negative density dependent effects (Wright, 2002). According to Leigh et al. (2004), microhabitat specialization and disturbance appear insufficient to

maintain alpha-diversity of trees in tropical forests, and there is a positive influence of larger areas covered by forests, where small populations have the chance to establish a new species.

Similarly, the disturbance and generation of new habitats that occurred during the uplift of the Andes ranges, was proposed as a major influence in the diversification of Neotropical plants. Gentry (1982) related the differences in familial composition to historical and ecological factors. He postulated the existence of two main centers of distribution in the Neotropics: Northern Andes and Central Amazonia. In each region, only certain families underwent processes of species diversification and, for this reason, present day floras in these two regions have an overrepresentation of certain families, in terms of species richness. Families with predominantly herb and shrub species tend to be diverse in Northwest South America (such as Costaceae, Gesneriaceae, Heliconiaceae, Zingiberaceae), while tree families are represented by many species in Central Amazonia (e.g. Burseraceae, Chrysobalanaceae, Lecythidaceae, Sapotaceae).

The most extreme extinction rates have been associated to drastic changes in global conditions (Benton & Twitchett, 2003), and local extinctions of particular plant species can also be caused by small changes in ecological conditions (Tilman & Lehman, 2001). Good examples of local extinctions come from studies of forest fragmentation, where changes in conditions, reductions in population numbers, and the extinction of mutualistic species tend to accelerate plant extinction rates and lower diversity (D'Angelo et al., 2004; Laurance et al., 2002). Therefore, even though fragmentation sets barriers to gene flow between populations, a process that might facilitate allopatric speciation and hence diversity (e.g. Haffer, 1969; Prance, 1982), evolutionary rates may be slow enough to allow differentiation of viable populations in such fragmented habitats.

Migration and colonization rates of trees have been estimated for temperate but not often for tropical regions. For instance, fossil pollen from northern latitudes has indicated rapid colonization rates unrelated with life history traits (i.e. dispersal kernels), which suggests that the colonization front was similarly limited to all plant species by climatic or geographic factors (Clark, 1998). Few studies have focused on colonization fronts in tropical plants, and these studies also suggest a large potential of rapid migration in these ecosystems (e.g. Charles-Dominique et al., 2003). In fact, the present geographic distributions of tropical plants show large variations in size, with some species restricted to particular sites, and other species with wide distributions (e.g. Henderson et al., 1995). This variation is consistent with the idea of rapid migration rates to areas with good climatic conditions, which may then be followed by local extinctions in less favorable periods, and low beta-diversity in western Amazonian forests (Condit et al., 2002). Although molecular analysis may provide information suggesting population dynamics of colonization, extinction and recolonization, this has been reported only a few times (e.g. Dutech et al., 2003), and it is difficult to be sure that local extinctions were driven by ecological or by stochastic population factors (e.g. random variations in population size).

In order to assess the relative importance of ecological vs. stochastic factors, several studies have quantified the proportion of the variation in floristic comparisons that can be attributed to ecological factors, then, the remaining variance in floristic patterns can be attributed to history or to chance (Tuomisto & Ruokolainen, 1997). On the other hand, neutral theories based on stochastic processes modeling community structure, predict a

negative relationship between floristic affinity and geographical distance (Hubbell, 2001). In fact, some studies using abundance of individuals between plant groups showed that floristic affinities between sites decrease with geographical distance at some regional scales (Terborgh & Andressen, 1998; Tuomisto et al., 2003). However, these studies do not rule out the influence of ecological factors. In fact, several studies have found significant contributions of geographical distance and ecological factors in explaining patterns of floristic similarity (Chust et al., 2006; Plotkin et al., 2000; Pyke et al., 2001; Tuomisto et al., 2003).

All lowland rain forests in the Neotropics have floras with similar familial compositions (Gentry, 1988). This has been explained by the common origin of the most important families, which differentiated long before the separation of Gondwanaland (Gentry, 1982). Furthermore, lowland Neotropical forests have not been greatly influenced by the invasion of predominantly temperate families. Thus, plant families such as Leguminosae, Annonaceae, Lauraceae, Rubiaceae, Moraceae, Myristicaceae, Sapotaceae, Melicaceae, Palmae, Euphorbiaceae and Bignoniaceae are common in almost all Neotropical lowland forests (Gentry, 1988). However, there is variation in floristic composition among particular localities, and predominant plant families are not always the same among different regions. Gentry (1990) pointed out that macro-ecological factors (e.g. soil quality, rainfall patterns, pollination syndromes) are important in determining floristic composition and affinities of different areas. Based on a qualitative comparison of four florulas, he showed differences in families and habitat composition, which were explained mostly by broad categorization of ecological conditions. For instance, the richest taxa in hyper-humid sites corresponded to families with high representation of epiphytes such as Orchidaceae, Araceae, and Piperaceae, while Leguminosae dominated at other places. The aim of this study is to make a quantitative floristic comparison based on the patterns of species richness in families and genera for more than twenty tropical areas, and to correlate floristic similarities with ecological and stochastic factors (e.g. geographical distance). We attempted to test the significance and relative roles of ecological and stochastic factors from the following predictions. If floristic similarities are significantly affected by ecological variables we expected: 1) to find sites of similar conditions grouped together in ordination analyses, and 2) a significant correlation between matrices of floristic similarity and ecological factors in Mantel tests (Mantel, 1967). On the other hand, according to the hypothesis that floristic composition is determined by chance, we expected to find: 1) agglomeration of close-by sites in the ordination, and 2) a positive correlation between geographical distance and floristic dissimilarity.

2. Methods

2.1 Localities

We searched the literature of florulas in lowland Neotropical areas, and included all places with appropriate macro-ecological information and good collection effort. We obtained a database of 26 sites for families and 25 sites for genera (Fig 1). In order to avoid biased inventories due to small sampling effort, we only included humid forests with at least 1,000 species reported, and dry forest with more than 500 species. We searched for geographic coordinates of each site to estimate the geographic distance between sites (calculated as a distance along the earth curvature). When the florula corresponded to a large area, we used

the centroid of the area to calculate the geographic distances to other places. The ecological conditions for each site were also extracted from the literature and from databases. We included information on average annual rainfall, average number of dry months (months with precipitation lower than 100 mm), and temperature for the 26 locations included in the analyses (Table 1).

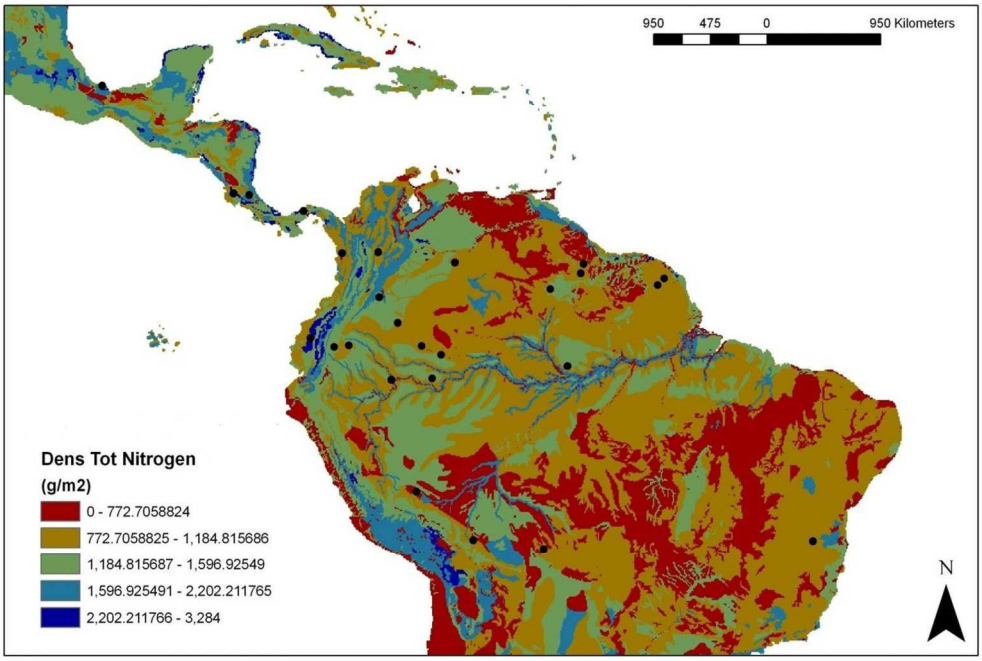


Fig. 1. Map of the neotropical region showing the location of the analyzed florulas, superimposed on a map of nitrogen content in the soils (from a geochemical and ecological database, ORNL DAAC, http://daac.ornl.gov/).

Site	Rainfall (mm)	Dry mo.	Temp (°C)	Reference	Coordinates		
					Long	Lat.	
1.Iquitos (Perú)	2949	0	25.9	Vásquez, 1997	73.30	3.50	S
2.Rio Palenque (Ecuador)	2650	0	23	Dodson & Gentry, 1978	79.40	0.40	S
3.La Selva (Costa Rica)	3962	0	25.8	Hammel & Grayum, 1982	84.00	10.40	N
4.Choco (Colombia)	6573	0	27	Forero & Gentry, 1989	77.00	6.00	N
5.Caqueta (Colombia)	3060	0	25.7	Duivenvoorden, 1996	71.00	1.00	S
6.Jatun Sacha (Ecuador)				http://www.mobot.org/MOBOT/research/ecuador/jatun/checklist.shtml	77.6	1.07	S

Site	Rainfall (mm)	Dry mo.	Temp (°C)	Reference	Coordinates		
					Long	Lat.	
7.Leticia (Colombia)	3215	0	25.8	Rudas & Prieto, 1998	70.20	3.40	S
8.Tuxtlas (Mexico)	4725	1	23.2	Ibarra-Manriquez & Sinaca-Colin, 1995	95.10	18.60	N
9.Tinigua (Colombia)	2702	2	26	Stevenson et al., 2000	74.20	2.70	N
10.Nouragues (French Guyana)	3124	2	27	Forget, 1994	52.70	4.10	N
11. Iwokrama (French Guyana)	2200	2		www.iwokrama.org	59.00	4.50	N
12.Mabura Hill (French Guyana)	2700	2	25.9	Renske & ter Steege, 1998	58.80	5.20	N
13.Cocha Cashu (Perú)	2028	3	24	Gentry, 1990	71.40	11.90	S
14.Bahia (Brazil)	1502	3.5	24.5	Mori et al., 1983	41.50	15.60	S
15.Ducke (Brazil)	2186	4	26.7	Gentry, 1990	60.00	2.50	S
16.BCI (Panama)	2656	4	27	Gentry, 1990	79.90	9.20	N
17. Maracá (Brazil)	2300	5	26.5	Thompson, 1992; Moskovits, 1985	61.30	3.30	N
18.Saul (French Guyana)	2413	6	27.1	Mori & Boom, 1987	53.20	3.60	N
19. Beni (Bolivia)	2550	2.5		Smith & Killeen, 1998	67.12	15.53	S
20.Las Quinchas (Colombia)	2654.7	0.5	27.8	Balcazar-Vargas et al., 2000	74.27	6.05	N
21. Chiribiquete (Colombia)	4000	0		Cortés-B & Franco-R,1997	72.80	0.80	N
22.Tuparro (Colombia)	2708	4		Mendoza et al., 2004	68.50	5.28	N
23. Yasuni (Ecuador)	2717	0		Valencia, 2004	76.5	0.95	S
24.Caparú (Colombia)	4000	0		Clavijo et al., 2009	69.52	1.65	S
25.Sta Rosa (Costa Rica)	1503	6	27.4	Enquist & Sullivan, 2001	85.20	10.50	N
26. Chiquitania (Bolivia)	1129	7	24.3	Killeen et al., 1998	61.80	16.20	S

Table 1. List of sites included in the study, their main climatic characteristics and location.

To facilitate comparison between localities, we used the floristic categories proposed by Foster and Hubbell (1990). Ferns are included as one group without differentiation of families, the three legume subfamilies (Papilionoidae, Mimosoidae and Caesalpinioidae) are presented as one (Fabaceae) and we did not treat Cecropiaceae within Urticaceae.

2.2 Climate and soil information

For each study site we obtained soil data from a geochemical and ecological database, ORNL DAAC (http://daac.ornl.gov/). Data were collected in the field, by satellite or generated by models. We chose 7 variables that describe soil properties: soil-carbon density (kg/m^2), profile available water capacity (mm), total nitrogen density (g/m^2), bulk density (g/cm3), field capacity (mm) (PsiFC=-10 kPa), thermal capacity (J/m3/K) (Theta=0.00 %v/v), and wilting point (mm) (PsiWP=-1500 kPa).

We characterized each of our study sites with 25 climatic variables found in WorldClim (http://www.worldclim.org; Hijmans et al., 2005). These bioclimatic variables are derived from monthly rain values and temperature, and represent annual trends. We included limiting environmental factors such as the temperature of the coldest and the warmest month, the rainfall of the 3 rainiest, and driest months. Additionally, the information for the number of dry months was taken from the field database or from the literature, because this variable explains a large part of the variation on maximal diversity of plants in the Amazon (Ter Steege et al., 2003).

We characterized each of the study sites in terms of soil and climate variables by spatially locating their area using the ArcGis program (http://www.arcgis.com/). Then, we quantified the weighted average of each variable for each site, depending on the characteristics of each polygon. We used this average as the value for each variable to comparison between the sites.

2.3 Floristic analysis

We ranked families and genera within each locality because the collection efforts were dissimilar between florulas, thus, it was not possible to quantify the vegetation by the absolute number of species. We included the 20 families with the highest number of species for each location. We assigned ranks to the families in the list (i.e. the most species-rich family in the list got a value of 20, the second a value of 19, and so on). The same was done for the top 22 genera in each locality. Then, we calculated an index of floristic similarity between sites based on these ranks (Stevenson, 2004):

$$D_{ab} = \sum_{i} \left| \text{rank } i_a - \text{rank } i_b \right| / (n(n+1)) \quad (1)$$

where, D_{ab} the floristic distance for each pair of localities (a and b) was the sum of the absolute differences between ranks. Then, 'i' was each of the families in the list included in both localities and 'n' is the number of families included (20 in this case). The division by n(n+1) standardizes the index between 1 and 0. High values (close to 1) indicated higher floristic differences. For instance, shared families that have high ranks in both localities contribute little to the index, while a high-ranking family from one locality that is absent in the other contributes the most. This index was used for one of the matrices (floristic matrix)

that we then used in Mantel Tests (Mantel, 1967). We also used this index for the 22 richest genera in each site. The cut off was generated as a tradeoff between increasing sampling size and avoiding sites with little information.

2.4 Statistical analysis

First, we ran a correlation analysis between the 26 environmental and soil variables to exclude redundant variables. Then we kept only variables which were not highly correlated with other independent variables ($r > 0.6$, Appendix 1).

We ordinated the localities according to the initial ranks using Nonmetric Multidimensional Scaling (NMS) in PCORD (Pc-Ord for Windows, Multivariate Analysis of Ecological Data. 5 version). We ran different analyses for family and genus information (Terborgh & Andresen, 1998). We did not make analyses at the species level because these comparisons could be compromised if species are misidentified, or if the same species is given a different name just because of its geographic location. To estimate floristic similarity, we used Euclidian distances from the rank matrix using PCORD. We allowed 20 runs for the NMS analysis, which used Euclidean distances. *A posteriori*, we determined the families (or genera) and the ecological factors that showed the highest correlation coefficients with the two main axes of the ordination, and according to the critical value of the Pearson's r (> 0.33) (Acton, 1966). Relevant families/genera and ecological factors can be graphically overlaid on the ordination.

To determine whether the observed patterns in the ordination were explained by geographical distances and/or ecological factors, we performed Mantel tests to evaluate the relationship between three different matrices for the 26 locations. The first matrix was a floristic distance matrix constructed from the ranks described above (either families or genera). The second matrix contained the values of climate and soil variables associated to each site. A third distance matrix included the Euclidean distances between the localities based on ecological factors and the distance from the young mountains (Andes and Central American ridges up to 1000m), as a proxy to relatively fertile sedimentation soils (Gentry, 1990).

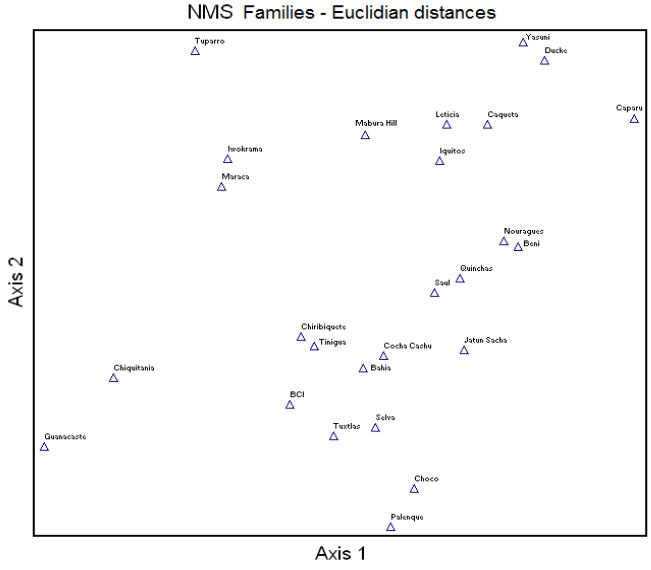
The subsequent Mantel Tests were ran to evaluate the interdependency of the independent variables that we had chosen. Thus, we constructed distance matrices (differences between places for each variable), and we made comparisons between each pair of matrices to determine if the observed patterns in the ordination were correlated with geographic distances or with ecological factors. These correlations are an important step to identify general pattern variations, but they cannot estimate how important each variable is in relation to the effects of other ones. For this reason, from each distance matrix between variables, we first did Mantel Tests to evaluate the relation between the different variables and the floristic distance. We then identified the variables that better explained the floristic distance. We ran partial Mantel tests while holding the geographical distances constant to observe how much variation in the floristic distance was explained by it. The mantel Tests were made with Excel Mantel Stats (XLStats, Statistical Software for MS Excel), and the significance of Mantel coefficients was tested via permutation tests with 10000 iterations.

3. Results

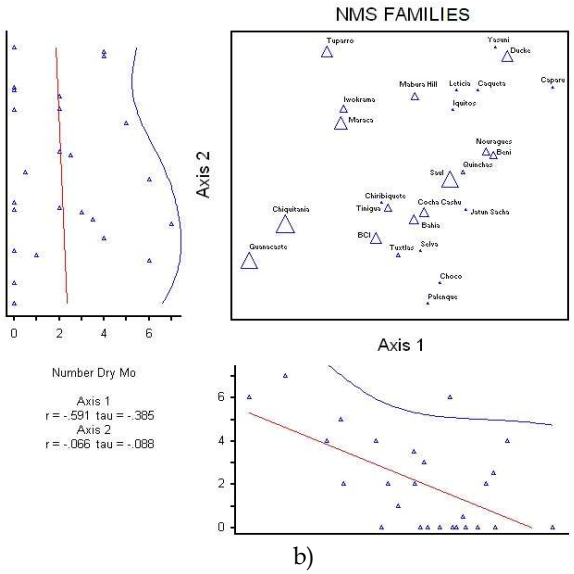
3.1 Family level comparisons

We found a wide spread of the 26 localities in the ordination based on floristic similarities (Fig 2). The main ecological variables associated with the arrangement of sites were rainfall and temperature. In particular, we found that the two driest sites are located at the lower left corner of the ordination, and high values corresponded mainly to wet sites with short dry seasons. Therefore, the x axis of the ordination showed a high negative correlation with the number of dry months (Fig 2.b). Most sites in the upper right corner of the ordination corresponded to rainy Amazonian and Guyannan sites, relatively far from the Andean and Central American mountains. These regions usually have nutrient-poor soils; however, we did not find any significant correlation between ordination axes and soil traits (Table 1). The two sites with lowest values in the y-axis corresponded to hyper-humid forests in the Choco biogeographic region.

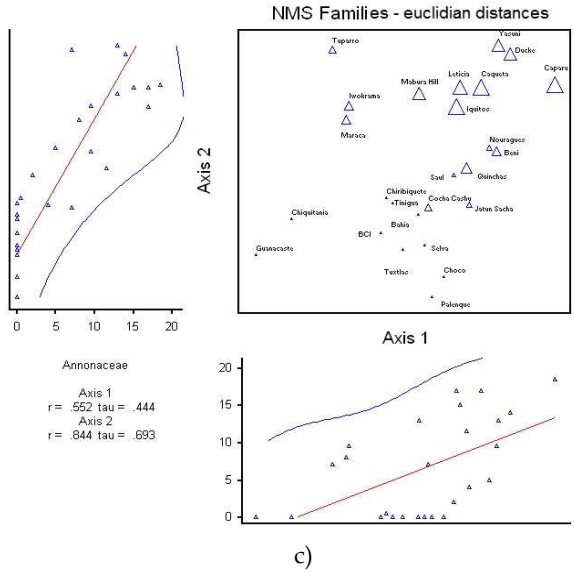
We found that the distribution of sites in the ordination was highly correlated with how rich are particular plant families in species (Table 2.a). For instance, the sites where Annonaceae was highly speciose, were located in the upper right corner of the floristic ordination (Figure 2c). We found a similar pattern for Lauraceae, Chrysobalanaceae, Clusiaceae and Sapotaceae. We also found that Bignoniaceae, Poaceae and Asteraceae were species rich families in the dry sites, showing a negative correlation with axis 1 (Table 2a). We also found a negative association between the number of species of Orchidaceae and Piperaceae and the axis 2 (Table 2a), mainly due to the richness in rainy forest in the Choco biogeographical region.



a)



b)



c)

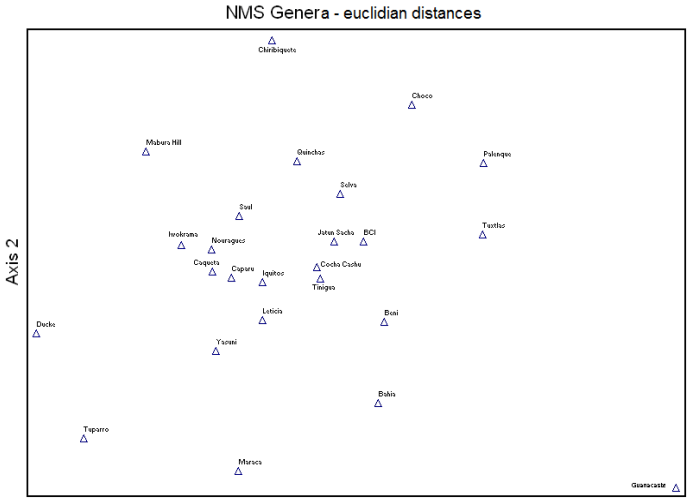
Fig. 2. NMS ordination of the 26 Neotropical localities, according to floristic affinities in terms of the number of species per family (a). In (b) the number of dry months for each site in the ordination is represented by the size of the triangle (a bigger size triangle indicates a longer dry season). The graphic also indicates the relation between the number of dry months and the two axes of the ordination. As an example, the number of species of the Annonaceae family is indicated in (c) again, by the size of the triangle. In this case the family is highly correlated with axis 2.

Even though we found that floristic dissimilarities among locations were correlated with ecological variables, we did not find that floristic affinities at the family level were associated with the geographical distances between them. Using Mantel tests, we obtained a significant association for three climatic variables (i.e. number of dry months, maximum temperature of the warmest month, and the mean day temperature; Table 3a). We obtained the same results in Mantel tests, even when the geographical distances were held constant, again showing a small effect of the geographic distance, and the largest effect from the number of dry months.

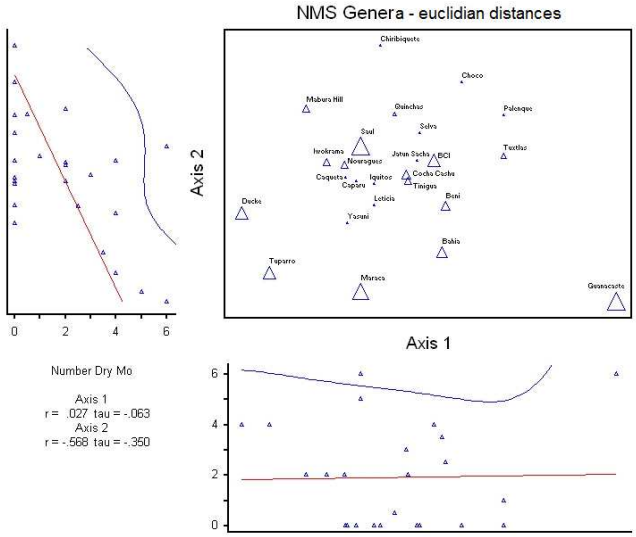
3.2 Genus level comparisons

In the ordination of the 25 localities using their similarities in genera composition, we found an atypical composition for the Costa Rican locality of Guanacaste (Fig 3.a), which was characterized by an extended dry season (Fig 3.b). The distribution of sites in the ordination was highly correlated with some plant genera (Table 2.b). The most influential genera showed a positive correlation with axis 1, and correspond to species-rich genera that are well represented in Guanacaste as *Desmodium* (Fig 3.c), *Hyptis, Ipomoea, Sida, Acacia, Capparis, Lonchocarpus and Mimosa* (Table 2.b.). *Eschweilera, Pouteria, Licania*, in contrast, showed negative correlations with axis 1, while *Trichomanes, Psychotria* and *Cassearia* were highly correlated with axis 2.

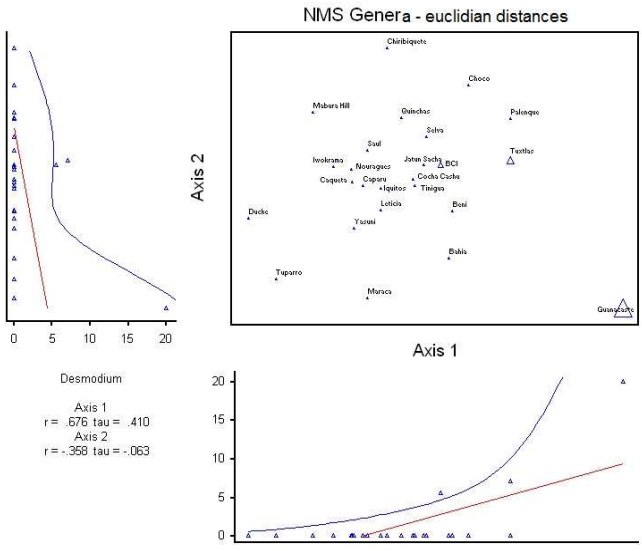
We found that floristic dissimilarities among the locations were correlated with macro ecological descriptors of the forests. Using Mantel tests, we found a significant correlation between the floristic and several climatic variables. In this case, the number of dry months again showed the highest correlation (e.g., Table 1b, Fig. 3b). The partial Mantel Tests showed that controlling for the geographic distance did not affect the effect of ecological variables.



a)



b)



c)

Fig. 3. NMS ordination of the 25 Neotropical localities according to the number of species per genera (a), and (b) the relation between the number of dry months in the ordination from the floristic affinities, in terms of species richness per genera. A bigger size triangle indicates longer duration of the dry season, and the graphics indicate a relation between the number of dry months and the two ordination axis. One of the genera with the highest correlation with axis 1 is *Desmodium* and it is mostly present in Guanacaste (c).

	Axis 1	Axis 2
	R	R
Annonaceae	0.552	0.844
Lauraceae	0.562	0.753
Chrysobalanaceae	0.252	0.627
Clusiaceae	0.422	0.607
Sapotaceae	0.619	0.523
Bignoniaceae	-0.619	0.011
Cyperaceae	-0.66	-0.002
Poaceae	-0.758	-0.392
Orchidaceae	-0.193	-0.626
Piperaceae	0.167	-0.722
Solanaceae	-0.209	-0.759
Asteraceae	-0.456	-0.832

a)

	Axis 1	Axis 2
	R	R
Desmodium	0.676	-0.358
Hyptis	0.665	-0.321
Ipomea	0.608	-0.416
Acacia	0.604	-0.430
Trichomanes	-0.069	0.636
Psychotria	-0.094	0.542
Solanum	0.592	-0.005
Acalypha	0.590	-0.420
Calliandra	0.590	-0.420
Capparis	0.590	-0.420
Cassia	0.590	-0.420
Lonchocarpus	0.590	-0.420
Mimosa	0.590	-0.420
Sida	0.590	-0.420
Piper	0.566	0.396
Croton	0.555	-0.396
Casearia	-0.248	-0.639
Pouteria	-0.525	0.009
Miconia	-0.601	0.004
Eschweilera	-0.604	0.09
Licania	-0.796	-0.238

b)

Table 2. Most dominant families (a) and genera (b), that are correlated with the sites distribution of the ordination.

	r(AB)	p-value
Number of dry months	0.245	< 0.001
Maximum To warmest month	0.179	0.002
Mean diurnal temperature	0.170	0.003
Distance to mountains	0.049	0.388
Temperature seasonality	0.106	0.053
Annual precipitation	0.077	0.166
Geographical distance	0.069	0.208
Total nitrogen density	0.016	0.768
Field capacity	-0.032	0.432
PAWC	-0.051	0.368

a)

	r(AB)	p-value
Number dry months	0.242	< 0.01
Maximum To warmest month	0.340	< 0.01
Geographical distance	0.269	< 0.01
Seasonality in temperature	0.268	< 0.01
Distance to mountains	0.210	< 0.01
Annual precipitation	0.167	< 0.01
Mean diurnal temperature	-0.032	0.437
Total nitrogen density	0.050	0.223
Field capacity	-0.053	0.200
PAWC	-0.014	0.740

b)

Table 3. Results of the bivariate Mantel Tests of each variable vs floristic distance for families (a) and for genera (b). The highlighted variables were the ones with a significant value.

4. Discussion

Our quantitative results support Gentry's ideas (1982, 1988, 1990) that floristic affinities in terms of species richness are determined mainly by ecological factors. Analyses at both the familial and generic levels showed significant correlations between ecological factors (i.e.

the number of dry months), and floristic affinities based on patterns of species richness. Interestingly, an analysis of plant diversity in Amazonia has also pointed to the duration of the dry season as the most important variable explaining maximum diversity (Ter Steege et al., 2003). It is possible that ecological variables related to temperature should have been important if highland forests were included, since temperature, altitude above sea level, and floristic affinities are well correlated (Gentry, 1988; 1995). Although the estimated amount of nitrogen in the soil was not highly correlated with floristic affinities in our analyses, we still think that nutrients in the soil may affect floristic composition. For instance, the fact that distance to young Andean and Central American mountains was correlated with the affinity of species richness within genera suggests that areas with similar sedimentation history (Latrubesse et al., 2010), show similar floristic composition. In addition, it is difficult to quantify soil nutrients at the spatial scale of florulas, and the spatial distribution of phosphorus, perhaps the most important nutrient in the soil for tropical plants, is not available at the spatial scales applied in this study.

The main families driving their placement in the first axis of the ordination differ in their dispersal systems and habit types. For instance, the most negatively correlated families were Poaceae, Cyperaceae, Bignoniaceae and Asteraceae, all characterized by abiotic seed dispersal and herbaceous and vine habits (Heywood et al., 2007). In contrast, the most positively correlated families were Sapotaceae, Lauraceae, Annonaceae, represented by trees with fleshy fruits dispersed by animals. The second axis shows the same dichotomy, but includes additional families of fleshy fruited species (Chrysobalanaceae) and wind dispersed species (Orchidaceae), both commonly found in humid forests (Gentry, 1995). These results suggest that particular families have functional traits that make them well suited for particular ecological settings and may coexist in places where they have reproductive advantages in comparison to other plant strategies. In fact, it is well established that large seeds are common in tree species (Foster & Janson, 1985), because large seeds have establishment advantages under closed canopy forests. In contrast, herbs and shrubs tend to have small seeds and are frequently represented in savannas, forest edges, and open canopy forests (Laurance et al., 2002; Stevenson & Rodriguez, 2008). However, biogeographical history might also influence the patters just described, since the large seeded, animal dispersed families represented by trees might have diversified in central Amazonia (Gentry, 1982; Stropp et al., 2009). Therefore, analyses of the plant traits promoting the establishment under particular conditions should control for phylogenetic and biogeographic history.

Similarly, at the genus level, the first axis of the ordination was negatively correlated with genera of large seeded animal dispersed seeds (*Licania* and *Eschweilera*), while it showed a high positive correlation with abiotically dispersed plants mainly represented by shrubs and vines (e.g., *Hyptis, Ipomea, Acacia, Acalypha* and *Calliandra*). However, it also includes genera dispersed by small animals such as birds and bats (*Miconia, Solanum* and *Capparis*), which are the most common seed dispersers in fragments and disturbed habitats (Pizo, 2004; Terborgh et al., 2008). The first axis was also positively correlated with the number of species of *Desmodium*, a genus dispersed in the fur of animals. These comparisons suggest that the patters of species richness might depend on ecological factors, such as the occurrence of dispersal agents and regeneration requirements.

The analyses at the genus level also showed a significant correlation between geographical distance and floristic affinity, as predicted by stochastic processes (Hubbell, 2001). Therefore, chance and mass-effects also play roles in the structure of plant communities in lowland Neotropical forests, and this effect seems to be more evident at low taxonomic scales. However, comparisons at the species level are more complicated, due to differences in the collection efforts and ambiguities in species determination, even though preliminary observations at the specific level also suggest a strong influence of ecological factors. For example, when the flora that we are more familiar with (Tinigua National Park, Stevenson et al., 2000) is compared to species lists of other Neotropical localities, we observed that the most similar sites correspond to western Amazonian localities with a dry period (i.e. Iquitos and Cocha Cashu). These sites are also very close to Tinigua in the generic ordination (Fig. 2), and not far away, though mixed, with other sites in the familial analysis (Fig. 1). These results could be better explained by ecological factors than by stochastic or historic events. Tinigua, Iquitos, and Cocha Cashu have 2-3 mo. dry seasons, and the three sites have relatively fertile soils because they have a greater influence of sedimentation from Andean soils. However, patches of forest on white sands are also common in the Iquitos area (Fine et al., 2006). Moreover, some of the same species are dominant at these localities, for instance, Foster's (1990) description of the floodplain at Cocha Cashu points to the dominance of *Guarea guidonia* and *Cecropia membranacea* in the early stages in riverine succession. These two species are not only the most important species in the flooded forests at Tinigua, but are also dominant in early succession processes (Stevenson et al., 2004), and *Heliconia marginata* dominates the understory in both places. Recent beaches are colonized mainly by *Tessaria integrifolia* and *Gynerium sagitatum* in both Cocha Cashu and Tinigua (Terborgh, 1983; Hirabuki et al., 1991).

The high floristic similarity between Tinigua and Cocha Cashu does not support the refuge theory, suggested originally by Haffer (1969) for Neotropical birds, and applied by Prance (1982) to the distribution of plant taxa. This theory proposed that in periods of increased aridity during the Pleistocene, populations were split into small patches of forests (refuges), where speciation occurred, followed by re-colonization of the forest. Haffer suggested that the actual distribution of species should therefore reflect the location of Pleistocene refuges. At least four refuges have been proposed for the upper Amazon basin, with Tinigua and Cocha Cashu near to two different refuges. If the present distribution of plant species originated in different refuges, then the flora at Tinigua and Cocha Cashu should be very different given the proximity to different refuges and the large geographical distance between the two places, but that is not the case. Interestingly, intermediate places such as Amazonian Ecuador, where there is no dry season, differ from Tinigua and Cocha Cashu in floristic composition. Thus our results provide futher evidence against the refuge theory (Colinvaux, 2005).

In summary, contrary to neutral theories, we can affirm that current and past macro-ecological factors have played significant roles determining the patterns of species richness in Neotropical lowland forests. Our analyses showed a minor effect of stochastic factors, but significant at some levels (i.e. genus). Does this mean that Neotropical plant communities are structured by niche differences? Although we did not address this question here, we think that this is not necessarily the case. For example, the fact that families with high

representation of epiphytes dominate florulas in very humid sites does not imply that all species are partitioning the resources. On the contrary, the vast number of co-occurring species suggests that conditions are good enough to allow many species to coexist, in spite of using similar resources and ecological strategies (e.g., dispersal systems and establishment requirements). Thus, some degree of stochasticity in population dynamics and speciation patterns may occur nested within the controlling macro-ecological factors, as well as past ecological conditions (Stropp et al., 2009). Perhaps we should not be too worried about trying to understand how many species live in present-day tropical forests, since the fossil record shows that many more species can coexist under the appropriate climatic conditions (Jaramillo et al., 2006).

5. Conclusion

We compared information on 26 lowland Neotropical florulas, in order to assess which processes are correlated with the patterns of floristic similarities, based on plant species richness within families and genera. The results at the family level indicated that floristic similarity is significantly correlated with ecological factors (e.g., rainfall patterns, temperature and the distance to young mountains as a proxy of sedimentation processes), but is not correlated with geographical distance. At the genus level, again, ecological factors were highly correlated with floristic similarity. However, at this level geographical distance was also significantly correlated with floristic similarity. These quantitative results support Gentry's theory which states that floristic affinities, in terms of patterns of species richness, are determined mainly by ecological factors. However, stochastic processes seem to play a minor but significant role, given that the most species rich genera were similar between close-by areas, as predicted by neutral models. Our findings and an accumulating body of evidence show that forest composition does change along environmental gradients (e.g., Bohlman et al., 2008; Coronado et al., 2009; Engelbrecht et al., 2007; Pitman et al., 2008: Tuomisto, 2006), in spite of the occurrence of widely distributed species along Neotropical forests (Bohlman et al., 2008; Condit et al., 2002). This emphasizes the relevance of protecting in areas of high human preference, because they are usually located in particular ecological settings and floristic composition. It is clear that human impacts, such as deforestation, have been prevalent in areas of high crop and livestock productivity (Madriñan et al. 2007), that include a set of unique native species. Therefore, a holistic approach for biodiversity conservation should provide the protection of forest in all ecological settings, including sites with high quality soils and productivity.

6. Acknowledgment

We thank the department of Biological Sciences and the Faculty of Sciences at Universidad de Los Andes, for the support to conduct this investigation. We thank Diana Guzman for comments and corrections.

7. Appendix 1

Correlation analysis among the 26 environmental and soil variables. Excluded variables that were associated with a correlation index of more than 0.6 are shown in grey.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
1. Shriveling point	1																									
2. Total Nitrogen density	-0.548	1																								
3. Thermal conductivity	0.230	-0.813	1																							
4. Soil humidity	0.06	-0.24	0.00	1.00																						
5. Field capacity	0.87	-0.58	0.20	0.54	1.00																					
6. Apparent soil density	0.23	-0.81	1.00	0.00	0.19	1.00																				
7. Soil carbon density	-0.68	0.95	-0.75	-0.34	-0.74	-0.75	1.00																			
8. Mean annual temperature	-0.01	0.10	-0.06	-0.24	-0.13	-0.06	0.07	1.00																		
9. Daytime mean temperature	0.18	-0.46	0.37	0.37	0.34	0.37	-0.49	-0.43	1.00																	
10. Isothermality	0.24	-0.11	-0.06	0.01	0.21	-0.05	-0.14	0.42	-0.15	1.00																
11. Seasonal temperature	-0.21	-0.01	0.14	0.16	-0.10	0.14	0.02	-0.58	0.44	-0.87	1.00															
12. Temperature of hottest month	0.00	-0.07	0.15	-0.05	-0.02	0.15	-0.13	0.74	0.07	-0.09	-0.03	1.00														
13. Lowest temperature of coldest month	0.00	0.23	-0.21	-0.27	-0.14	-0.21	0.20	0.90	-0.71	0.56	-0.77	0.44	1.00													
14. Annual temperature range	0.00	-0.30	0.32	0.28	0.14	0.32	-0.29	-0.60	0.82	-0.68	0.84	0.06	-0.87	1.00												
15. Mean temperature of most humid quartile	-0.20	0.14	-0.06	-0.11	-0.22	-0.05	0.11	0.92	-0.32	0.27	-0.37	0.76	0.75	-0.42	1.00											
16. Mean temperature of driest quartile	0.06	0.12	-0.11	-0.18	-0.04	-0.10	0.08	0.94	-0.58	0.40	-0.62	0.65	0.94	-0.69	0.82	1.00										
17. Mean temperature of hottest quartile	-0.12	0.17	-0.06	-0.22	-0.21	-0.06	0.14	0.95	-0.39	0.16	-0.33	0.85	0.79	-0.42	0.93	0.89	1.00									
18. Mean temperature of coldest quartile	0.04	0.12	-0.12	-0.23	-0.08	-0.12	0.07	0.96	-0.50	0.61	-0.79	0.57	0.96	-0.75	0.83	0.93	0.84	1.00								
19. Annual precipitation	0.04	-0.06	-0.14	0.15	0.11	-0.14	-0.02	0.16	-0.37	0.42	-0.41	-0.14	0.36	-0.48	0.10	0.31	0.06	0.27	1.00							
20. Precipitation of most humid month	-0.22	0.24	-0.37	0.18	-0.09	-0.37	0.29	0.18	-0.47	0.07	-0.20	0.04	0.36	-0.38	0.18	0.38	0.19	0.23	0.81	1.00						
21. Precipitation of driest month	0.23	-0.25	0.05	0.18	0.28	0.06	-0.24	0.06	-0.19	0.63	-0.49	-0.33	0.25	-0.46	0.00	0.14	-0.12	0.20	0.83	0.41	1.00					
22. Seasonal precipitation	-0.43	0.32	-0.08	0.00	-0.37	-0.08	0.32	-0.19	0.23	-0.60	0.53	0.23	-0.32	0.49	-0.08	-0.25	0.00	-0.31	-0.60	-0.12	-0.82	1.00				
23. Precipitation of most humid quartile	-0.21	0.21	-0.38	0.27	-0.04	-0.38	0.24	0.15	-0.41	0.14	-0.21	-0.01	0.32	-0.36	0.15	0.32	0.14	0.21	0.86	0.98	0.51	-0.19	1.00			
24. Precipitation of driest quartile	0.24	-0.26	0.06	0.17	0.29	0.06	-0.24	0.10	-0.22	0.65	-0.52	-0.29	0.30	-0.49	0.03	0.20	-0.07	0.25	0.87	0.45	0.99	-0.84	0.54	1.00		
25. Precipitation of hottest quartile	-0.29	0.21	-0.36	0.44	-0.03	-0.36	0.21	-0.29	0.02	0.21	-0.02	-0.44	-0.15	-0.07	-0.15	-0.25	-0.33	-0.20	0.61	0.50	0.60	-0.29	0.61	0.57	1.00	
26. Precipitation of coldest quartile	0.33	-0.17	-0.04	-0.08	0.24	-0.04	-0.15	0.41	-0.38	0.51	-0.56	0.12	0.57	-0.56	0.20	0.54	0.29	0.50	0.81	0.61	0.65	-0.56	0.63	0.71	0.15	1.00

8. References

Acton, F. S. (1966). *Analysis of straight line data*. Dover, New York.

Balcázar-Vargas, M. P., Rangel-Ch., J.O. & Linares-C, E.L. (2000). Diversidad florística de la Serranía de Las Quinchas, Magdalena Medio (Colombia). *Caldasia,* 22, pp. (191-224)

Benton, M. J. & Twitchett, R. J. (2003). How to kill (almost) all life: the end-Permian extinction event. *Trends in Ecology & Evolution,* 18, pp. (358-365)

Bohlman, S. A., Laurance, W. F., Laurance, S. G., Nascimento, H. E. M., Fearnside, P. M., Ana, A. (2008). Importance of soils, topography and geographic distance in structuring central Amazonian tree communities. *Journal of Vegetation Science* 19, pp. (863-874)

Charles-Dominique, P., Chave, J., Dubois, M. A., De Granville, J. J., Riera, B. & Vezzoli, C. (2003). Colonization front of the understorey palm *Astrocaryum sciophilum* in a pristine rain forest of French Guiana. *Global Ecology and Biogeography,* 12, pp. (237-24)

Chust, G., Chave, J., Condit, R., Aguilar, S., Lao, S. & Perez, R. (2006). Determinants and spatial modeling of tree beta-diversity in a tropical forest landscape in Panama. *Journal of Vegetation Science,* 17, pp. (83-92)

Clark, J. S. (1998). Why trees migrate so fast: Confronting theory with dispersal biology and the paleorecord. *American Naturalist,* 152, pp. (204-224)

Clavijo, L., Betancur, J. & Cérdenas, D. (2009). Plantas con flores de la Estación Biológica Mosiro-Itajura-Caparú, Vaupés, Amazonia colombiana, In: *Estación Biológica Mosito Itajura-Caparú. Biodiversidad en el territorio del Yagojé-Apapporis*, G. Alarcón-Nieto & E. Palacios, pp. (55-97). Conservación Internacional Colombia, Bogotá

Colinvaux, P. (2005). The Pleistocene vector of neotropical diversity. In: *Tropical rainforests: past, present and future*, Bermingham, E. Dick C. W. Moritz C., pp (78-106). University of Chicago Press, Chicago.

Coronado, E. N., Baker, T. R., Phillips, O. L., Pitman, N. C. A., Pennington, R. T., Vasquez-Martinez, R., Monteagudo, A., Mogollon, H., Davila-Cardozo, N., Rios, M., Garcia-Villacorta, R., Valderrama, E., Ahuite, M., Huamantupa, I., Neill, D. A., Laurance, W. F., Nascimento, H. E. M., de Almeida, S. S., Killeen, T. J., Arroyo, L., Nunez, P., Freitas Alvarado, L. (2009). Multi-scale comparisons of tree composition in Amazonian terra firme forests. *Biogeosciences,* 6, pp. (2719-2731)

Condit, R., Pitman, N., Leigh, E. G., Chave, J., Terborgh, J., Foster, R. B., Nunez, P., Aguilar, S., Valencia, R., Villa, G., Muller-Landau, H. C., Losos, E. & Hubbell, S. P. (2002). Beta-diversity in tropical forest trees. *Science,* 295, pp. (666-669)

Cortes, R. & Franco, P. (1997). Análisis panbiogeografico de la flora de Chiribiquete, Colombia. *Caldasia*, 19, 3, pp. (465-478)

D'Angelo, S. A., Andrade, A. C. S., Laurance, S. G., Laurance, W. F. & Mesquita, R. C. G. (2004). Inferred causes of tree mortality in fragmented and intact Amazonian forests. *Journal of Tropical Ecology,* 20, pp. (243-246)

Dodson, C. & Gentry, A. H. (1978). Flora of the Rio Palenque Science Center. *Selbyana,* 4, pp. (1-623)

Duivenvoorden, J. F. (1996). Patterns of tree species richness in rain forests of the middle Caqueta area, Colombia, NW Amazonia. *Biotropica*, 28, 2, pp. (142-158)

Dutech, C., Maggia, L., Tardy, C., Joly, H. I. & Jarne, P. (2003). Tracking a genetic signal of extinction-recolonization events in a neotropical tree species: *Vouacapoua americana* aublet in French Guiana. *Evolution,* 57, pp. (2753-2764)

Engelbrecht, B. M. J., Comita, L. S., Condit, R., Kursar, T. A., Tyree, M. T., Turner, B. L., Hubbell, S. P. (2007). Drought sensitivity shapes species distribution patterns in tropical forests. *Nature* 447, pp. (80-82)

Enquist, B. J. & Sullivan, J. J. (2001). *Vegetative key and descriptions of tree species of the tropical dry forest of upland Sector Santa Rosa, Area de Coservación Guanacaste, Costa Rica*, Retrieved from: http://acguanacaste.ac.cr/paginas_especie/plantae_online/EnquistSullivanTreeKey.pdf

Fine, P. V. A., Miller, Z. J., Mesones, I.,, Irazuzta, S., Appel, H. M., Stevens, M. H. H., Saaksjarvi, I., Schultz, L. C. & Coley, P. D. (2006). The growth-defense trade-off and habitat specialization by plants in Amazonian forests. *Ecology,* 87, pp. (150-162)

Fine, P. V. A. & Ree, R. H. (2006). Evidence for a time-integrated species-area effect on the latitudinal gradient in tree diversity. *American Naturalist* 168, 6, pp. (796-804)

Forero, E. & Gentry, A. H. (1989). *Lista Anotada de las plantas del departamento del Chocó, Colombia. Bogotá, Instituto de Ciencias Naturales - Museo de Historia Natural -*, Universidad Nacional de Colombia, Bogotá

Forget, P. M. (1994). Recruitment Pattern of *Vouacapoua americana* (Caesalpiniaceae), a Rodent-Dispersed Tree Species in French Guiana. *Biotropica*, 26, 4, pp. (408-419)

Foster, R. B. (1990). The Floristic Composition of the Rio Manu Floodplain Forest, In: *Four Neotropical Rainforests*, A. H. Gentry, pp. (99-111), Yale University Press, New Haven

Foster, R. B., & Hubbell, S. P. (1990). The Floristic Composition of the Barro Colorado Island Forest, In: *Four Neotropical Rainforests*, A. H. Gentry, pp. (85-89), Yale University Press, New Haven

Foster, S. A., & Janson, C. H. (1985). The relationship between seed size and establishment conditions in tropical woody-plants. *Ecology*, 66, pp. (773-780)

Gentry, A. H. (1982). Neotropical floristic diversity: phytogeographical connections between Central and South America, Pleistocene climatic fluctuations, or an accident of the Andean orogeny? *Annals of the Missouri Botanical Garden*, 69, pp. (557-593)

Gentry, A. H. (1988). Changes in plant community diversity and floristic composition on geographical and environmental gradients. *Annals of the Missouri Botanical Garden,* 75, pp. (1-34)

Gentry, A. H. (1990). Floristic similarities and differences between Southern Central America and Upper and Central Amazonia, In: *Four Neotropical Rainforests*, A. H. Gentry, pp. (141-157), Yale University Press, New Haven

Gentry, A. H. (1995). Patterns of diversity and floristic composition in neotropical montane forest. In: *Biodiversity and conservartion of neotropical montane forests.* Churchill S. P., Baslev, H., Forero E. & Lutyn, J. L., pp. (103-126). The New York Botanical Garden. New York

Gong, Y. B. & Huang, S. Q. (2011). Temporal stability of pollinator preference in an alpine plant community and its implications for the evolution of floral traits. *Oecologia,* 166, pp. (671-680)

Gravendeel, B., Smithson, A., Slik, F. J. W. & Schuiteman, A. (2004). Epiphytism and pollinator specialization: drivers for orchid diversity? *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences,* 359, pp. (1523-1535)

Haffer, J. (1969). Speciation in Amazonian forest birds. *Science,* 165, pp. (131-137)

Hammel, B. E. & Grayum, M. H. (1982). Preliminary report on the flora project of La Selva Field Station, Costa Rica. *Annals of the Missouri Botanical Garden*, 69, 2, pp. (420-425)

Henderson, A., Galeano, G. & Bernal, R. (1995). *Field guide to the palms of the Americas,* Princeton University Press, Princeton, N.J, pp. (363)

Heywood, V, H., R. K. Brummitt, R. K., Culham A.& Seberg, O. (2007). *Flowering plant families of the world.* Royal Botanic Gardens, Kew, pp. (424)

Hijmans, R. J., S. E. Cameron, Parra, J. L., Jones, P. G. & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology,* 25, 15, pp. (1965-1978)

Hirabuki, Y., Takehara, A. & Hara, M. (1991) Some characteristics of fluvial soils along a riparian succession in the upper Colombian Amazon. *Field Studies of New World Monkeys La Macarena Colombia* 5, 17-24.

Hubbell, S. P. (2001). *The unified neutral theory of biodiversity and biogeography*, Princeton University Press, Princeton, N.J, pp. (375)

Ibarra-Manriquez, G. & Sinaca-Colin, S. (1995). Commented Checklist of Plants From the Los-Tuxtlas Biological Station, Veracruz, Mexico (Mimosaceae-Verbenaceae). Revista De Biologia Tropical, 44, 1, pp. (41-60)

Jaramillo, C., Rueda, M. J. & Mora, G. (2006). Cenozoic plant diversity in the Neotropics. *Science,* 311, pp. (1893-1896)

Killeen, T. J., Jardim, A., Mamani, F. & Rojas, N. (1998). Diversity, composition and structure of a tropical semideciduous forest in the Chiquitania region of Santa Cruz, Bolivia. *Journal of Tropical Ecology*, 14, pp. (803-827)

Kristiansen, T., J. C. Svenning, Pedersen, D., Eiserhardt, W. L., Grández, C. & Balslev, H. (2011). Local and regional palm (Arecaceae) species richness patterns and their cross-scale determinants in the western *Amazon. Journal of Ecology,* 99, pp. (1001-1015)

Latrubesse, E. M., Cozzuol, M., da Silva-Caminha, S. A. F., Rigsby, C. A., Absy, M. L. & Jaramillo, C. (2010). The Late Miocene paleogeography of the Amazon Basin and the evolution of the Amazon River system. *Earth-Science Reviews,* 99, pp. (99-124)

Laurance, W. F., Lovejoy, T. E., Vasconcelos, H. L., Bruna, E. M., Didham, R. K., Stouffer, P. C, Gascon, C., Bierregaard, R. O., Laurance, S. G. & Sampaio, E. (2002). Ecosystem decay of Amazonian forest fragments: A 22-year investigation. *Conservation Biology,* 16, pp. (605-618)

Leigh, E. G., Davidar, P., Dick, C. W., Puyravaud, J. P., Terborgh, J., ter Steege, H. & Wright, S.J. (2004). Why do some tropical forests have so many species of trees? *Biotropica,* 36, pp. (447-473)

Madriñan, L. F., Etter, A., Boxall, G. D., Ortega-Rubio, A. (2007). Tropical alluvial forest fragmentation in the eastern lowlands of Colombia (1939-1997). *Land Degradation & Development,* 18, pp. (199-208)

Mantel, N. (1967). The detection of disease clustering and a generalized regression approach. *Cancer Research,* 27, pp. (209–220).

Mendoza, H. (2004). *Caracterización florística y faunística del PNN El Tuparro*. Instituto Alexander von Humboldt, Bogotá

Mori, S. A. & Boom, B. M. (1987). The forest. *Memoirs of the New York Botanical Garden,* 44, pp. (9-29)

Mori, S. A., Boom, B. M., de Carvalho, A. M. & dos Santos, T. S. (1983). Southern Bahian Moist Forests. *Botanical Review,* 49, 2, pp. (155-232)

Moskovits, D. K. (1985). *The behavior and ecology of the two Amazonian tortoises, Geochelone carbonaria and Geochelone denticulata, in northwestern Brasil.* PhD thesis, The University of Chicago, Department of Biology, Chicago, pp. (328)

Pitman, N. C. A. Mogollon, H., Davila, N., Rios, M. Garcia-Villacorta, R., Guevara, J., Baker, T. R., Monteagudo, A., Phillips, O. L., Vasquez-Martinez, R., Ahuite, M., Aulestia, M., Cardenas, D., Ceron, C. E., Loizeau, P. A., Neill, D. A., Percy, N. V., Palacios, W. A., Spichiger, R, & Valderrama, E. (2008). Tree community change across 700 km of lowland Amazonian forest from the Andean foothills to Brazil. *Biotropica,* 40, pp. (525-535)

Pizo, M. A. (2004). Frugivory and habitat use by fruit-eating birds in a fragmented landscape of southeast Brazil. *Ornitologia Neotropical,* 15, pp. (117-126)

Plotkin, J. B., Potts, M. D., Leslie, N., Manokaran, N., LaFrankie, J. & Ashton, P. S. (2000). Species-area curves, spatial aggregation, and habitat specialization in tropical forests. *Journal of Theoretical Biology,* 207, pp. (81-99)

Prance, G. T. (1982) Forest refuges: evidence from woody angiosperms, In: *Biological divesification in the tropics*, G.T. Prance, pp. (137-158), Columbia University Press, New York.

Pyke, C. R., Condit, R., Aguilar, S. & Lao, S. (2001). Floristic composition across a climatic gradient in a neotropical lowland forest. *Journal of Vegetation Science,* 12, pp. (553-566)

Renske, C. & Ter Steege, H. (1998). Studies on the flora of the Guianas no. 89: The flora of the Mabura Hill area, Guyana. *Botanische Jahrbuecher fuer Systematik Pflanzengeschichte und Pflanzengeographie,* 120, 4, pp. (461-502)

Rudas, A. & Prieto, A. (1998). Analisis floristico del Parque Nacional Natural Amacayacu e Isla Mocagua, Amazonas (Colombia). *Caldasia,* 20, 2, pp. (142-172)

Smith, D. N. & Killeen, T. J. (1998). A comparison of the structure and composition of montane and lowland tropical forest in the Serrania Pilon Lajas, Beni, Bolivia, In: *Missouri Botanical Garden Webpage*, Available from: http://www.mobot.org/MOBOT/research/bolivia/pilonarticle/welcome.shtml

Stevenson, P. R. (2004). Phenological patterns of woody vegetation at Tinigua Park, Colombia: Methodological comparisons with emphasis on fruit production. *Caldasia,* 26, 1, pp. (125-150)

Stevenson, P. R., Quiñones, M. J. & Castellanos, M. C. (2000). *Guía de Frutos de los Bosques del Río Duda, Macarena, Colombia*, Asociación Para la Defensa de La Macarena – IUCN, Bogotá

Stevenson, P. R. & Rodríguez, M. E. (2008). Determinantes de la composición florística y efectos de borde en un fragmento de bosque en el Guaviare, Amazonia colombiana. *Colombia Forestal,* 11, pp. (5-17)

Stevenson, P. R., Suescun, M., and Quiñones, M. J. (2004). Characterization of forest types at the CIEM, Tinigua Park, Colombia. *Field Studies of Fauna and Flora Macarena Colombia,* 14, (1-20)

Stropp, J., Ter Steege, H. & Malhi, Y. (2009). Disentangling regional and local tree diversity in the Amazon. *Ecography,* 32, 1, pp. (46-54)

Ter Steege, H., Pitman, N., Sabatier, D., Castellanos, H., Van der Hout, P., Daly, D. C., Silveira, M., Phillips, O., Vasquez, R., Van Andel, T., Duivenvoorden, J., De Oliveira, A. A., Ek, R., Lilwah, R., Thomas, R., Van Essen, J., Baider, C., Maas, P., Mori, S., Terborgh, J., Vargas, P. N., Mogollon, H. & Morawetz, W. (2003). A spatial model of tree alpha-diversity and tree density for the Amazon. *Biodiversity and Conservation,* 12, pp. (2255-2277)

Terborgh, J. (1983) *Five new world primates*, Princeton University Press, Princeton, pp (260)

Terborgh, J. & Andresen, E. (1998) The composition of Amazonian forests: patterns at local and regional scales. *Journal of Tropical Ecology*, 14, pp. (645-664)

Terborgh, J., Nuñez-Iturri, G., Pitman, N. C. A., Valverde, F. H. C., Alvarez, P., Swamy, V., Pringle, E. G., Paine, C. E. T. (2008). Tree recruitment in an empty forest. Ecology, 89, pp (1757-1768)

Tilman, D. & Lehman, C. (2001). Human-caused environmental change: Impacts on plant diversity and evolution. *Proceedings of the National Academy of Sciences of the United States of America,* 98, pp. (5433-5440)

Thompson, J., Proctor, J., Viana, V., Milliken, W., Ratter, J. A. & Scott, D. A. (1992). Ecological studies on a lowland evergreen rain-forest on Maraca Island, Roraima, Brazil .1. Physical-environment, forest structure and leaf chemistry. *Journal of Ecology*, 80, pp. (689-703)

Tuomisto, H. (2006). Edaphic niche differentiation among Polybotrya ferns in western Amazonia: implications for coexistence and speciation. *Ecography,* 29, pp. (273-284)

Tuomisto, H. & Ruokolainen, K. (1997). The role of ecological knowledge in explaining biogeography and biodiversity in Amazonia. *Biodiversity and Conservation,* 6, pp. (347-357)

Tuomisto, H., Ruokolainen, K. & Yli-Halla, M. (2003). Dispersal, environment, and floristic variation of western Amazonian forests. *Science,* 299, pp. (241-244)

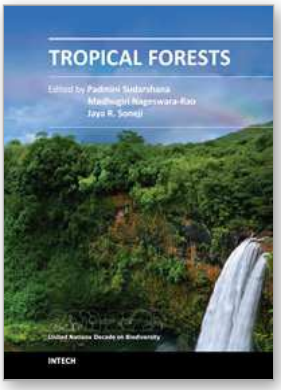
Valencia R. (2004). Yasuni forest dynamics plot, Ecuador. In: Losos EC, Leigh J, Giles E (eds). Tropical Forest Diversity and Dynamism: Findings from a Large-Scale Plot Network. University of Chicago Press: Chicago. pp (609–628)

Vásquez, R, Rudas LLeras, A. & Taylor, C. M. (1997*). Flórula de las reservas biológicas de Iquitos, Perú: Allpahuayo-Mishana, Explornapo Camp, Explorama Lodge,* Missouri Botanical Garden Press, St. Louis, pp. (1046)

Waser, N. M., Chittka L, Price, M. V., Williams, N. M. & Ollerton, J. (1996). Generalization in pollination systems, and why it matters. *Ecology,* 77, pp. (1043-1060)

Wright, J. S. (2002). Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia,* 130, pp. (1-14)

WorldClim – Global Climate Data, Available from: http://www.worldclim.org



Tropical Forests

Edited by Dr. Padmini Sudarshana

ISBN 978-953-51-0255-7
Hard cover, 388 pages
Publisher InTech
Published online 14, March, 2012
Published in print edition March, 2012

The astounding richness and biodiversity of tropical forests is rapidly dwindling. This has severely altered the vital biogeochemical cycles of carbon, phosphorus, nitrogen etc. and has led to the change in global climate and pristine natural ecosystems. In this elegant book, we have defined "Tropical Forests" broadly, into five different themes: (1) tropical forest structure, synergy, synthesis, (2) tropical forest fragmentation, (3) impact of anthropogenic pressure, (4) Geographic Information System and remote sensing, and (5) tropical forest protection and process. The cutting-edge synthesis, detailed current reviews, several original data-rich case studies, recent experiments/experiences from leading scientists across the world are presented as unique chapters. Though, the chapters differ noticeably in the geographic focus, diverse ecosystems, time and approach, they share these five important themes and help in understanding, educating, and creating awareness on the role of "Tropical Forests" for the very survival of mankind, climate change, and the diversity of biota across the globe. This book will be of great use to the students, scientists, ecologists, population and conservation biologists, and forest managers across the globe.

How to reference

In order to correctly reference this scholarly work, feel free to copy and paste the following:

Pablo R. Stevenson, María Clara Castellanos and Juliana Agudelo T. (2012). Patterns of Plant Species Richness Within Families and Genera in Lowland Neotropical Forests: Are Similarities Related to Ecological Factors or to Chance?, Tropical Forests, Dr. Padmini Sudarshana (Ed.), ISBN: 978-953-51-0255-7, InTech, Available from: http://www.intechopen.com/books/tropical-forests/patterns-of-plant-species-richness-within-families-and-genera-in-lowland-neotropical-forests-are-the

INTECH
open science | open minds

InTech Europe
University Campus STeP Ri
Slavka Krautzeka 83/A
51000 Rijeka, Croatia
Phone: +385 (51) 770 447
Fax: +385 (51) 686 166
www.intechopen.com

InTech China
Unit 405, Office Block, Hotel Equatorial Shanghai
No.65, Yan An Road (West), Shanghai, 200040, China
中国上海市延安西路65号上海国际贵都大饭店办公楼405单元
Phone: +86-21-62489820
Fax: +86-21-62489821